



Ocean Solutions to Address Climate Change and Its Effects on Marine Ecosystems

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The Paris Agreement target of limiting global surface warming to 1.5–2°C compared to pre-industrial levels by 2100 will still heavily impact the ocean. While ambitious mitigation and adaptation are both needed, the ocean provides major opportunities for action to reduce climate change globally and its impacts on vital ecosystems and ecosystem services. A comprehensive and systematic assessment of 13 global- and local-scale, ocean-based measures was performed to help steer the development and implementation of technologies and actions toward a sustainable outcome. We show that (1) all measures have tradeoffs and multiple criteria must be used for a comprehensive assessment of their potential, (2) greatest benefit is derived by combining global and local solutions, some of which could be implemented or scaled-up immediately, (3) some measures are too uncertain to be recommended yet, (4) political consistency must be achieved through effective cross-scale governance mechanisms, (5) scientific effort must focus on effectiveness, co-benefits, disbenefits, and costs of poorly tested as well as new and emerging measures.

Keywords: climate change, ocean acidification, ocean solutions, global, local, governance

INTRODUCTION

The ocean provides most of the life-supporting environment on the planet. It hosts a large portion of biodiversity, plays a major role in climate regulation, sustains a vibrant economy and contributes to food security worldwide. Severe impacts on key marine ecosystems and ecosystem services are projected in response to the future increase in global mean temperature and concurrent ocean acidification, deoxygenation, and sea-level rise (Hoegh-Guldberg et al., 2014; Pörtner et al., 2014; Gattuso et al., 2015). These impacts scale to CO₂ emissions: they will be considerably worse with a high emissions scenario than with a scenario that limits the temperature increase to 2°C relative to pre-industrial levels (Bopp et al., 2013). Current emission reduction pledges under the 2015 Paris Agreement (UNFCCC, 2015) are, however, insufficient to keep global temperature below +2°C in 2100 relative to pre-industrial level (Rogelj et al., 2016) and to reach targets for the United Nations Sustainable Development Goals. Increased ambition, with additional actions, is therefore required.

Further reductions in atmospheric greenhouse gas emissions are achievable through: (1) a shift from fossil fuels to renewable energy; (2) improved energy efficiency; (3) carbon capture and storage (CCS) at the point of CO₂ generation; and (4) the protection and enhancement of natural carbon sinks (Griscom et al., 2017; Rockström et al., 2017). The risk of failing to meet climate targets via emissions reduction has increased interest in solar radiation management (National Research Council, 2015b) and carbon dioxide removal from the atmosphere (National Research Council, 2015a; Williamson, 2016; Hansen et al., 2017). For example, the implementation of bioenergy with carbon capture and storage is a major component of a roadmap to reduce global emissions from ~40 Gt CO₂ year⁻¹ in 2020 to ~5 Gt CO₂ year⁻¹ by 2050 (Rockström et al., 2017). Such an ambitious roadmap, however, poses significant political, economic, and environmental challenges because of the land, water, and nutrient requirements to produce the biomass (potentially in competition with existing ecosystems, land use, and food production), the cost and feasibility of carbon capture and storage, and the fact that such systems have yet to be proven effective at the required scales (Anderson and Peters, 2016; Smith et al., 2016; Boysen et al., 2017). Additionally, and even under a successful mitigation scenario, impacts are expected at the local scale, hence the need for enhanced adaptation measures.

To date, policy responses to climate change and its impacts have largely focussed on land-based actions (Field and Mach, 2017) while relatively little attention has been paid to ocean-based potential (Rau et al., 2012; Billé et al., 2013), despite the recent launch of the Ocean Pathway initiative by the Presidency of the 23rd Conference of the Parties (COP23) of the United Nations Framework Convention on Climate Change (UNFCCC). The ocean already removes about 25% of anthropogenic CO₂ emissions (Le Quéré et al., 2018) and has the potential to remove and store much more (Rau, 2014). Thus, ocean-based actions could significantly

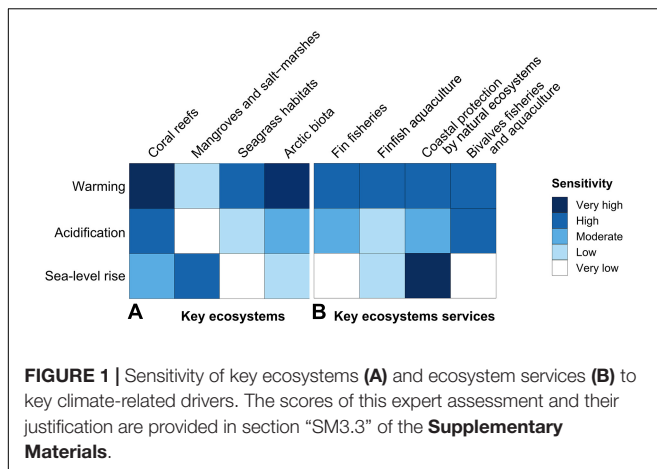
reduce the magnitude and rate of ocean warming, ocean acidification, and sea-level rise, as well as their impacts on marine ecosystems and ecosystem services. They could also play a significant role in helping to reduce global warming and its impacts on the non-ocean surface of the planet – and on human society. However, there may be associated risks to ocean life and people, and there is a lack of guidance for prioritizing ocean-based interventions since there has been relatively little research, development and deployment in this field. Important issues include determining the effectiveness of a given approach in countering changes in climate drivers and/or impacts, possible spatial and temporal scales of deployment, associated positive and negative climate, environmental, economic, and societal impacts (Russell et al., 2012), and hence the implications for ethics, equity, and governance (Preston, 2013; Burns et al., 2016; Williamson and Bodle, 2016).

To fill this gap, we assess the potential of 13 categories of ocean-based measures or schemes to reduce climate-related drivers globally and/or locally (<~100 km²), as well as to reduce adverse impacts on selected, important and sensitive marine ecosystems and ecosystem services. The three drivers considered are ocean warming, ocean acidification and sea-level rise, although others such as hypoxia, extreme events, and changes in storminess and precipitation can also be important. We focus on four ecosystems and habitats (warm-water coral reefs, mangroves and salt-marshes, seagrass beds, and Arctic biota) and four ecosystem services (finfish fisheries, fish aquaculture, coastal protection, and bivalve fisheries and aquaculture), which are particularly vulnerable to climate impacts and are critical for livelihoods and food security. The potential of each ocean-based measure is assessed in terms of the following eight environmental, technological, social, and economic criteria: (1) potential effectiveness to increase net carbon uptake and moderate ocean warming, ocean acidification, and sea level rise; (2) technological readiness; (3) lead time until full potential effectiveness; (4) duration of benefits; (5) co-benefits; (6) disbenefits; (7) cost effectiveness; and (8) governability from an international perspective. This expert assessment is based on an extensive literature review and is supported by **Supplementary Materials (SM)** that provide details on the terminology, assessment methods, results, and supporting literature.

CLIMATE-RELATED SENSITIVITY OF OCEAN ECOSYSTEM AND ECOSYSTEM SERVICES

Key Ecosystems Investigated

Ecosystems have different sensitivities to ocean warming, ocean acidification and sea-level rise (**Figure 1A** and section “SM3.3” of the **Supplementary Materials**). Interactions between drivers can be complex: additive, synergistic, or antagonistic (Crain et al., 2008). There are big gaps in multiple-drivers research (Crain et al., 2008; Riebesell and Gattuso, 2015) but experimental



strategies to assess the biological ramifications of multiple drivers of global ocean change have become available (Boyd et al., 2018).

Of the four ecosystems or habitats considered here, coral reefs and Arctic biota are the most imminently threatened and will be affected to a greater degree sooner than others, with high risk that key functions will be lost globally, as identified in the 5th assessment report (AR5) of the Intergovernmental Panel on Climate Change (IPCC) (Hoegh-Guldberg et al., 2014; Pörtner et al., 2014). Coral reefs are very sensitive to ocean warming and acidification (Hoegh-Guldberg et al., 2007; Gattuso et al., 2014; Hughes et al., 2017a). They have suffered extensive losses in the past three decades due to high sea surface temperature combined with local stressors such as overfishing, destructive fishing, coastal development, and pollution. All projections indicate that the thermal conditions driving major losses will increase in frequency and exceed thresholds for the majority of reefs by 2050 (Gattuso et al., 2014; Pörtner et al., 2014). Over the 21st century under the high emissions Representative Concentration Pathway RCP8.5 scenario (van Vuuren et al., 2011), 99% of the world's coral reefs are expected to experience annual severe bleaching due to thermal stress (van Hooidonk et al., 2016). The thermal sensitivity of coral reefs is compounded by ocean acidification (Hoegh-Guldberg et al., 2014), which diminishes coral growth and calcification (Albright et al., 2018) and can lead to increased bioerosion and vulnerability to storm damage (Andersson and Gledhill, 2013).

Arctic biota are also highly sensitive to climate change, particularly ice-associated biota that are rapidly declining in Arctic summers (Wassmann et al., 2010; Pörtner et al., 2014; Kohlbach et al., 2017). Within the Arctic, ecosystem responses vary greatly depending on ambient variability, degree of warming, and nutrient advection (Hunt et al., 2016). Warming and freshening may also impact ecosystem production by differentially increasing respiration rates and reducing nutrient supply (Duarte et al., 2012) as well as enhancing the degree of ocean acidification due to freshening (Pörtner et al., 2014). Arctic organisms that seem particularly

sensitive to ocean acidification include calcifiers such as bivalves and planktonic pteropods that are key links in ocean food webs (Comeau et al., 2010; Duarte et al., 2012).

Mangroves and saltmarshes are highly sensitive to sea-level rise (Kirwan and Megonigal, 2013; Lovelock et al., 2015), particularly where coastal development and steep topography block landward migration and insufficient sediment is delivered to support accretion. A preliminary global modeling effort suggests that a 50 cm sea-level rise by 2100 would result in a loss of 46 to 59% of global coastal wetlands (up to 78% loss under 110 cm rise), but losses are sensitive to assumptions about human coastal development and may be reduced if additional tidal hydrodynamic feedbacks are included (Spencer et al., 2016). Warming and acidification are not projected to have significant direct effects on mangroves and saltmarshes, but may have positive or negative effects at local scales due to changes in species composition, phenology, productivity, and latitudinal range of distribution (Ward et al., 2016).

Temperate seagrass ecosystems are sensitive to ocean warming. For example, the thermal regime of the Mediterranean Sea already exceeds the upper thermal limit of the endemic *Posidonia oceanica* in some areas (Marbà and Duarte, 2010; Jordà et al., 2012). Seagrass and fleshy algae may expand in Arctic regions with warming and loss of ice cover (Krause-Jensen and Duarte, 2014). Some may benefit from carbonate chemistry changes associated with ocean acidification as their photosynthesis is CO₂-limited (Raven and Beardall, 2014) but sensitive calcifiers growing in the meadows are negatively impacted (Martin et al., 2008).

Key Ecosystem Services Investigated

The ecosystem services considered in this study are all highly sensitive to ocean warming (Weatherdon et al., 2016; Figure 1B and section “SM3.3” of the **Supplementary Materials**). Global potential fisheries catches and species turnover, for instance, are projected to decrease by about 3 Mt and increase by 10%, respectively, for every 1°C of global surface warming (Cheung et al., 2016). These patterns are similar for finfish and shellfish aquaculture, as ~90% of current finfish and shellfish mariculture production is from open-water farming where environmental conditions closely match those in the nearby ocean (Callaway et al., 2012). Shellfish fisheries and mariculture, in particular, are threatened by the combined effects of warming (Mackenzie et al., 2014), ocean acidification (Barton et al., 2012; Gazeau et al., 2013) and deoxygenation (Gobler et al., 2014). Despite possible genetic adaptation over generations (Thomsen et al., 2017), impacts on shellfish are expected to be high to very high when CO₂ concentrations exceed those projected for 2100 in the low to moderate RCP2.6 and 4.5 CO₂ emissions scenarios (Gattuso et al., 2015; Cooley et al., 2016). In addition, finfish mariculture often focuses on high trophic level species that are dependent on wild capture fisheries for feed (Troell et al., 2014) and some operations still largely rely on wild captured fish fry and

juveniles (Diana, 2009). Thus, mariculture is likely to be subject to similar climatic stresses as fish stocks in the wild.

The sensitivity of coastal protection, notably wave attenuation and shoreline stabilization, to climate-related drivers differs for each ecosystem considered (Spalding et al., 2014). The cumulative impacts of increasing sea-surface temperature, ocean acidification, and non-climatic stressors such as land-based pollution reduce reefs' ability to keep pace with sea-level rise (Yates et al., 2017). The consequences of sea-level rise on biologically structured coastal ecosystems raise concerns as these habitats are estimated to currently reduce wave height by 30 to 90% (in order of highest to lowest wave reduction: coral reefs, saltmarshes, mangroves, and seagrasses) (Fonseca and Cahalan, 1992; Duarte et al., 2013; Ferrario et al., 2014; Narayan et al., 2016). Historical global losses in coastal ecosystems [30 to 50% for mangroves since the 1940s, 29% for seagrass since 1879, 25% for saltmarshes since the 1800s (Waycott et al., 2009; Mcleod et al., 2011)] and degradation of coral reefs [30–75% since prehuman times (Pandolfi et al., 2003)] have already reduced their potential to provide ecosystem services. Projections suggest that 90% of coral reefs worldwide could be lost if warming exceeds 1.5°C (Frieler et al., 2013).

OCEAN-BASED SOLUTIONS

Four types of actions to reduce the scale and impacts of climate change are considered (Figure 2): (1) reduction of atmospheric greenhouse gas concentrations, (2) solar radiation management, (3) protection of biota and ecosystems, and (4) manipulation of biological and ecological adaptation. The actions in the first two categories (referred to as global actions hereafter, although some forms of solar radiation management could be local) aim to either reduce the main cause of climate change at the global scale (primarily the increase in atmospheric CO₂ concentration) or to counteract warming through increasing albedo in the atmosphere or at the Earth's surface, thereby increasing the proportion of solar radiation that is reflected back to space. The actions in the other two categories (referred to as local actions hereafter) aim to reduce the risk of climate change impacts locally, either by reducing the locally experienced drivers (site-specific acidification and warming, and relative sea-level rise) and/or reducing the sensitivity of organisms and ecosystems to these drivers (Bates et al., 2017; Cheung et al., 2017). *Vegetation* and *alkalinization* (see Box 1 and section "SM1" of the **Supplementary Materials** for descriptions) are evaluated for both global and local aims as they can be deployed globally to reduce changes in climate-related drivers and impacts, as well as locally to reduce the sensitivity of marine ecosystems and services to specific drivers such as relative sea-level rise and ocean acidification.

Other ocean-based measures have been proposed but little research has been conducted on their potential. They include large-scale seaweed aquaculture for supplementing cattle feed to reduce methane emissions and counteract acidification locally (Machado et al., 2016; Duarte, 2017). Abiotic methods of removing or stripping CO₂ from seawater have also been

proposed or demonstrated in the laboratory (Eisaman et al., 2012; Willauer et al., 2014; Koweek et al., 2016), as well as marine-based interventions that increase uptake and reduce emissions of other greenhouse gases such as CH₄ and N₂O (e.g., Poffenbarger et al., 2011; Stolaroff et al., 2012). Research and testing of new, unconventional methods of ocean and climate management are in their infancy, and additional methods are likely to emerge.

Whereas some of the solutions assessed here are still at a very-early or experimental stage, others have been implemented and refined over many decades, though not always specifically designed to address climate change impacts. The global implementation of *renewable energy*, *vegetation*, *eliminating overexploitation*, and *protection* exhibit a sharp acceleration in the past two decades (Figure 3). For example, global cumulative offshore wind potential has grown 3-fold in less than 5 years to reach 15,000 MW in 2016 (Global Wind Energy Council, 2016). MPAs now cover more than 3% of the global ocean (Boonzaier and Pauly, 2016), 7% of the overexploited fish stocks have been rebuilt (Kleisner et al., 2013) and the global area of avoided loss of mangroves has been estimated at 40,000 km² (Hamilton and Casey, 2016).

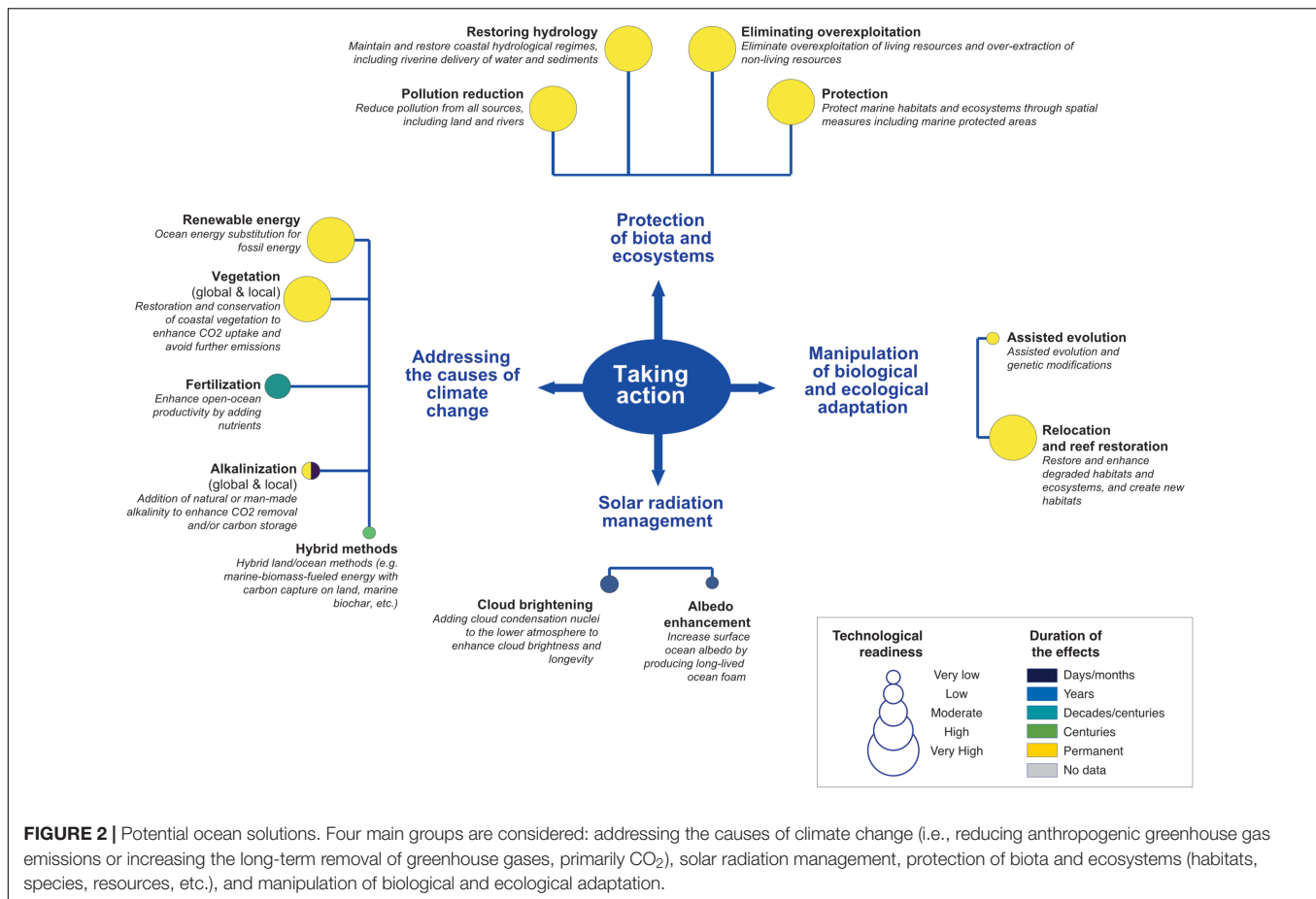
POTENTIAL TO REDUCE KEY OCEAN DRIVERS

Effectiveness of the Measures and Duration of Their Effects

To estimate effectiveness, we first assess the potential of each measure –assumed here to be implemented at its maximum physical capacity– to bridge the gap between the high-emissions trajectory (RCP8.5, our baseline scenario) and a stringent emission-reduction scenario (RCP2.6) expected to keep mean global temperature increase below 2°C by 2100 (van Vuuren et al., 2011) (see section "SM2" of the **Supplementary Materials**). The differences between RCP8.5 and RCP2.6 in the year 2100 are estimated to be ~1,400 Pg C for avoided emissions; ~2°C for reduced sea surface warming; ~0.25 pH units for avoided sea surface acidification; and a reduction in sea-level rise of between 0.26 and 1.1 m (Jones et al., 2013; DeConto and Pollard, 2016).

The effectiveness of the global measures is assessed in terms of maximum possible effectiveness to reduce ocean warming, ocean acidification, and sea-level rise (Figure 4A), and duration of the effect (Figure 4B). This maximum effectiveness is theoretical and almost certainly not achievable but provides the full potential of each approach. Two of the global solutions, *renewable energy* and *alkalinization*, stand out as having the highest theoretical potential for addressing all drivers (Figure 4A). This is obvious for *renewable energy* because of the enormous energy potential of tides, waves, ocean currents, and thermal stratification, estimated at up to 7,400 EJ year⁻¹ (Rogner et al., 2000; Lewis et al., 2011) and well exceeding future human energy needs. Any replacement of fossil fuels by marine renewables results in permanently avoided greenhouse gas emissions.

A similarly large and permanent intervention could be provided by large-scale *alkalinization*, by which CO₂ is consumed



and stored either as dissolved bicarbonate and carbonate ions or as precipitated calcium carbonate, neutralizing ocean acidity. However, the feasibility and benefits of doing this must be weighed against the financial costs and environmental impacts of mining or producing vast quantities of alkaline material, distributed at global scales, and the potential biotic impacts of the trace elements or contaminants that alkalinity might contain (Renforth and Henderson, 2017).

Land-ocean *hybrid methods* greatly expand the mitigation potential offered by either land-based or ocean-based approaches individually. For example, the use of marine biomass for bioenergy with carbon capture and storage (BECCS) fuel eliminates limitations on terrestrial fuel capacity posed by competition for land, water, and nutrients. In turn, conversion of CO₂ from land-based biomass energy to ocean alkalinity and subsequent storage in the ocean greatly expands CO₂ storage capacity and beneficial use (via countering ocean acidification) relative to more conventional CCS approaches. However, a comprehensive understanding of the full range of options, and their costs, benefits and tradeoffs requires further research (Rau, 2014).

Albedo enhancement also has a very large potential effectiveness in moderating warming (Figure 4A), as a relatively small enhancement of the albedo of the dark ocean surface by less than 0.05 could compensate the entire GHG-driven perturbation

in the Earth's radiation balance (Crook et al., 2016; Garciadiego Ortega and Evans, 2018). However, the duration of the effect is only as long as the albedo stays high, likely to be days to months for ocean foams (Figure 4B) and, as SRM in general, it does not limit ocean acidification as atmospheric CO₂ concentration remains elevated (Tjiputra et al., 2016). Similar considerations apply to marine *cloud brightening*, although modeling studies indicate more limited effectiveness (Kravitz et al., 2013; Stjern et al., 2017).

Other potential solutions face physical and/or biogeochemical limitations (Figure 4A). A global deployment of iron *fertilization* for 100 years could sequester a maximum of ~70 Pg C (ref. Aumont and Bopp, 2006) because other nutrient or light limitations occur when marine algae are iron-replete (Oschlies et al., 2010). Some measures demonstrate limited potential for reducing warming, acidification and sea-level rise at global scales, such as *vegetation* for instance. Even with very high carbon storage and avoided net emissions, the *vegetation* measure is constrained by the limited global area of potentially vegetated habitats, although with some scope to artificially expand that area; e.g., via seaweed aquaculture (Duarte et al., 2017; Hawken, 2017).

Local measures have a relatively low effectiveness to reduce warming, acidification, and sea-level rise at the global scale (Figure 4A). However, some have a high to very high effectiveness

BOX 1 | Ocean-based solutions. Measures that address the causes of global climate change either reduce anthropogenic greenhouse gas emissions or increase their long-term removal from the atmosphere. Five measures are considered in this group, including negative emissions technologies (see Minx et al., 2018) which are critical for achieving the long-term climate goals of the Paris Agreement (UNFCCC, 2015). (1) Ocean-based renewable energy (hereafter **renewable energy**) comprises the production of energy using offshore wind turbines and harvesting of energy from tides, waves, ocean currents, and thermal stratification (Pelc and Fujita, 2002). (2) The restoration and conservation of coastal vegetation (hereafter **vegetation**), primarily saltmarshes, mangroves and seagrasses (also referred to as “blue carbon ecosystems”), seeks to enhance their carbon sink capacity and avoid emissions from their existing large carbon stocks if degraded or destroyed (McLeod et al., 2011; Herr and Landis, 2016). This measure is considered not only in terms of global implementation – i.e., assuming theoretical worldwide conservation and restoration of all such habitats that have been degraded or lost due to human activities – but also local implementation, providing local mitigation and adaptation benefits in addition to other co-benefits. (3) **Fertilization** involves the artificial increase in the ocean’s primary production and, hence, carbon uptake by phytoplankton in the open ocean, to be achieved primarily by adding soluble iron to surface waters where it is currently lacking, mostly in mid-ocean gyres and the Southern Ocean (Aumont and Bopp, 2006). (4) **Alkalinization** describes the addition of a variety of alkaline substances that consume CO₂ and/or neutralize acidity (Rau, 2011; Renforth and Henderson, 2017), primarily achieved by raising the concentration of carbonate or hydroxide ions in surface waters, and thereby shifting the associated chemical equilibria in seawater to increase the oceanic uptake of atmospheric CO₂. The feasibility and effectiveness of adding alkalinity are considered at both global and local scales. In either case the alkalinity would be derived from land-based mineral or synthetic chemical sources or from locally available marine material (e.g., waste shells). The alkalinity would then require transport to and distribution within the marine environment. (5) Land-ocean **hybrid methods** include the use of the ocean and its sediments to store biomass, CO₂ or alkalinity derived from terrestrial sources. Examples are crop residue storage on the seafloor (Strand and Benford, 2009), marine storage of CO₂ from land-based bio-energy or from direct air capture of CO₂ (Sanz-Pérez et al., 2016) and conversion of such CO₂ to alkaline forms for ocean storage (Rau, 2011). **Hybrid methods** also include techniques involving marine-to-land transfers, such as using marine biomass to fuel biomass energy with carbon capture and storage (BECCS) on land or using such biomass to form biochar as a soil amendment.

Another area of action to counter global and ocean warming (but which does not directly address the greenhouse gas cause) is solar radiation management (SRM, also known as sunlight reflection methods). Several schemes were described, including stratospheric aerosol injection (National Research Council, 2015b). Two ocean-based schemes are considered here. (6) Marine cloud brightening (hereafter **cloud brightening**) involves the large-scale aerial spraying of seawater or other substances into the lower atmosphere to increase the amount of sunlight clouds reflect back into space (Latham et al., 2012; Kravitz et al., 2013). Sub-global implementation could also be considered (Latham et al., 2013). (7) Increased surface ocean albedo (hereafter **albedo enhancement**) is here considered to be achieved by long-lived ocean micro-bubbles or foams, produced either by commercial shipping (Crook et al., 2016) or by vessels dedicated to that task.

Four measures relate to the protection of biota and ecosystems. (8) **Reducing pollution** refers to decreasing release of anthropogenic, harmful substances. Pollution can exacerbate hypoxia and ocean acidification especially in coastal waters (Cai et al., 2011) while increasing the sensitivity of marine organisms and ecosystems to climate-related drivers (Alava et al., 2017). (9) Restoring hydrological regimes (**restoring hydrology**) relates to the maintenance and restoration of marine hydrological conditions, primarily in coastal waters, including both the tidal and riverine delivery of water and sediments, to alleviate local changes in climate-related drivers (Howard et al., 2017). (10) **Eliminating overexploitation** includes ensuring the harvest and extraction of living resources are within biologically safe limits for sustainable use by humans and to maintain ecosystem function and, in the case of non-living resources (e.g., sand and minerals), in levels that avoid irreversible ecological impacts. For example, in over-exploited ecosystems, pelagic species that are smaller and faster turnover generally increase in dominance (Cheung et al., 2007). Abundance of these pelagic species tends to track environmental conditions more closely than large demersal fishes (Winemiller, 2005), the latter are often depleted in over-exploited systems (Cheung et al., 2007). Thus, fisheries with increased dominance of pelagic species are generally more sensitive to changes in environmental conditions from climate change (Planque et al., 2010). Although species with higher turnover rates may theoretically have more capacity to adapt evolutionarily to environmental changes (Jones and Cheung, 2018), the scope and rate of such adaptive response for most fishes are unclear (Munday et al., 2013). Also, over-exploited fish stocks with largely reduced abundance may also have reduced genetic diversity and variability, and consequently the population will have a reduced scope for adaptation under climate change. (11) The protection of habitats and ecosystems (**protection**) refers to the conservation of habitats and ecosystems, primarily through marine protected areas (MPAs). For example, increased abundance of marine species is expected to enhance productivity of the surrounding areas which can help buffer against climate impacts and increase resilience (Roberts et al., 2017).

In the category “manipulation of biological and ecological adaptation” of organisms and ecosystems to the changing ocean conditions, two measures are assessed. (12) **Assisted evolution** involves large-scale genetic modification, captive breeding and release of organisms with enhanced stress tolerance (van Oppen et al., 2015). (13) **Relocation and reef restoration** involves not only the restoration of degraded coral and oyster reefs (e.g., van Oppen et al., 2017), but also their enhancement and active relocation, with the potential creation of new habitats and use of more resilient species or strains. Note that restoration and protection of vegetated coastal habitats (seagrasses, mangroves, and saltmarshes) is considered in the **vegetation** measure.

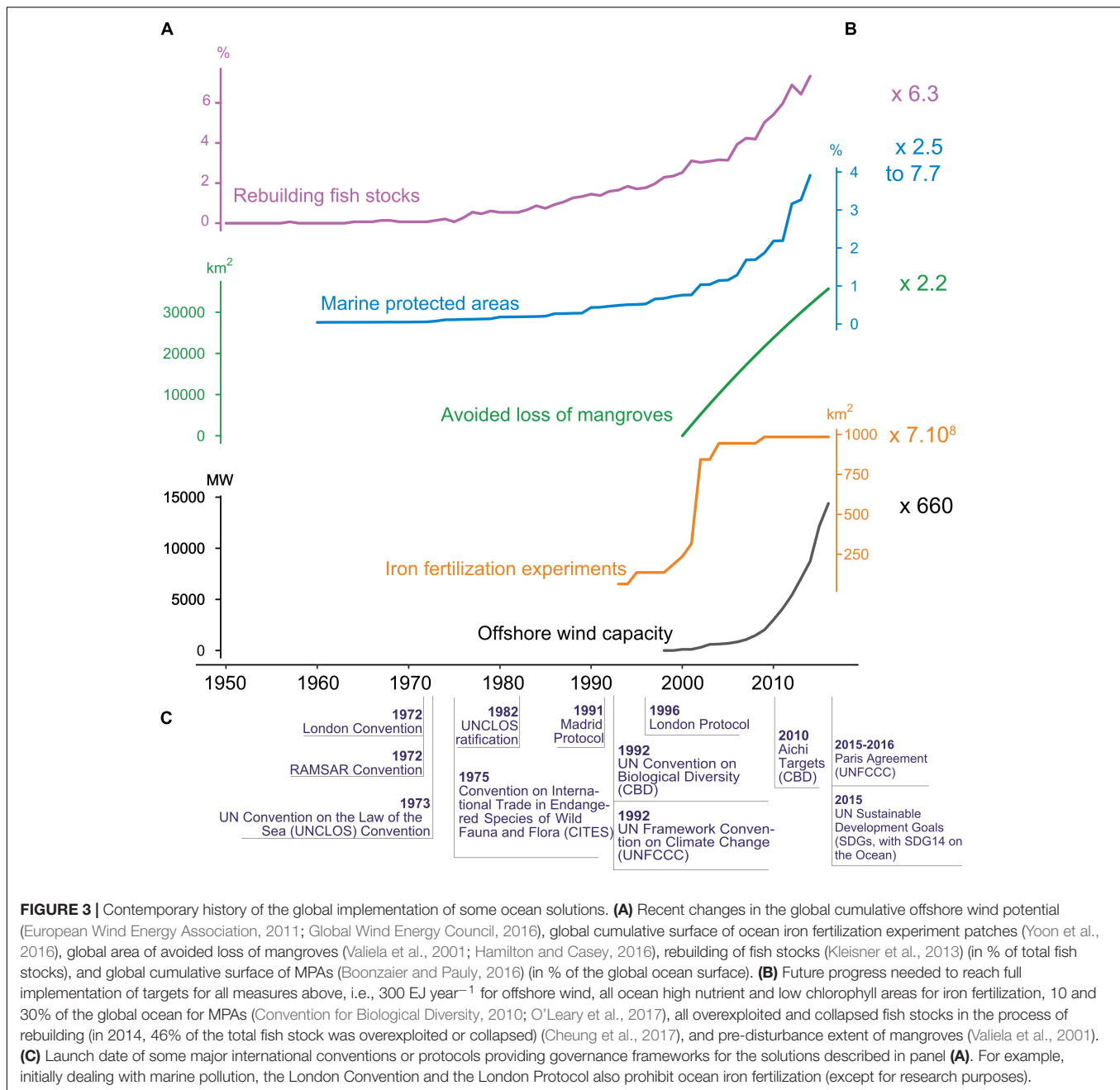
to moderate local ocean acidification (*pollution reduction* and *alkalinization*) and relative sea-level rise (*vegetation*, *protection*, *restoring hydrology*, as well as *relocation and reef restoration*).

The duration of the effects varies greatly between the different methods (**Figure 4B**). It is close to permanent for *renewables* as long as the infrastructure is maintained. The effects of protection are also considered permanent as long as MPAs are enforced, although future climate change will decrease their ability to provide climate mitigation and adaptation benefits (Bruno et al., 2018). The effects of *vegetation* can be close to permanent as long as these ecosystems are maintained or increased in the face of natural and anthropogenic pressures. In contrast, the effects of *fertilization* have a finite duration. Once iron fertilization is stopped, a large portion of the additional ocean carbon uptake will outgas back to the atmosphere on decadal to centennial time scales (Aumont and Bopp, 2006). By capturing and storing CO₂ for long time periods or permanently, *alkalinization* and

hybrids methods such as conversion of CO₂ to ocean alkalinity or marine BECCS generally have long duration of the effect. In contrast, the effect of *albedo enhancement* and *cloud brightening* is short-lived (days to weeks). The loss of most benefits following abrupt termination is a characteristic of all SRM schemes (Jones et al., 2013). It is projected to increase both ocean and land temperature velocities to unprecedented speeds (Trisos et al., 2018).

Technical Feasibility and Cost Effectiveness

Technical feasibility is evaluated by considering current technological readiness (ranging from schemes at the concept stage to schemes already deployed) and for lead time until full potential effectiveness, i.e., the time needed to reach full implementation (ranging from days to decades; see section



“SM2” of the **Supplementary Materials**). Two local measures have the highest technical feasibility (**Figure 4B**): *protection* and *restoring hydrology*. *Vegetation* (both global and local) and *renewable energy* also have a high technical feasibility, closely followed by *eliminating overexploitation*, *reducing pollution* and *relocation and reef restoration*. Five global schemes have the lowest technical feasibility: *fertilization*, *cloud brightening*, *alkalinization*, *albedo enhancement*, and *hybrid methods*. The local measure *assisted evolution* also scores very low on this criterion. These low scores generally reflect lack of testing and deployment at scale, thus they also possess high uncertainty.

The cost effectiveness of the global and local solutions is assessed, in US\$ per tonne of CO₂ emissions reduced and in US\$ per hectare of surface area of implementation, respectively (**Figure 4E** and section “SM3.5” of the **Supplementary Materials**). The costs considered here are best estimates from the literature for the direct monetary costs of implementation. The non-monetary costs of implementation are considered through assessing co-benefits, disbenefits, and governability, as discussed below. Since cost effectiveness is a relative metric, it does not reflect the effectiveness of a measure to reduce changes in the drivers. For instance, *cloud brightening* is cost-effective despite having a moderate maximum effectiveness to

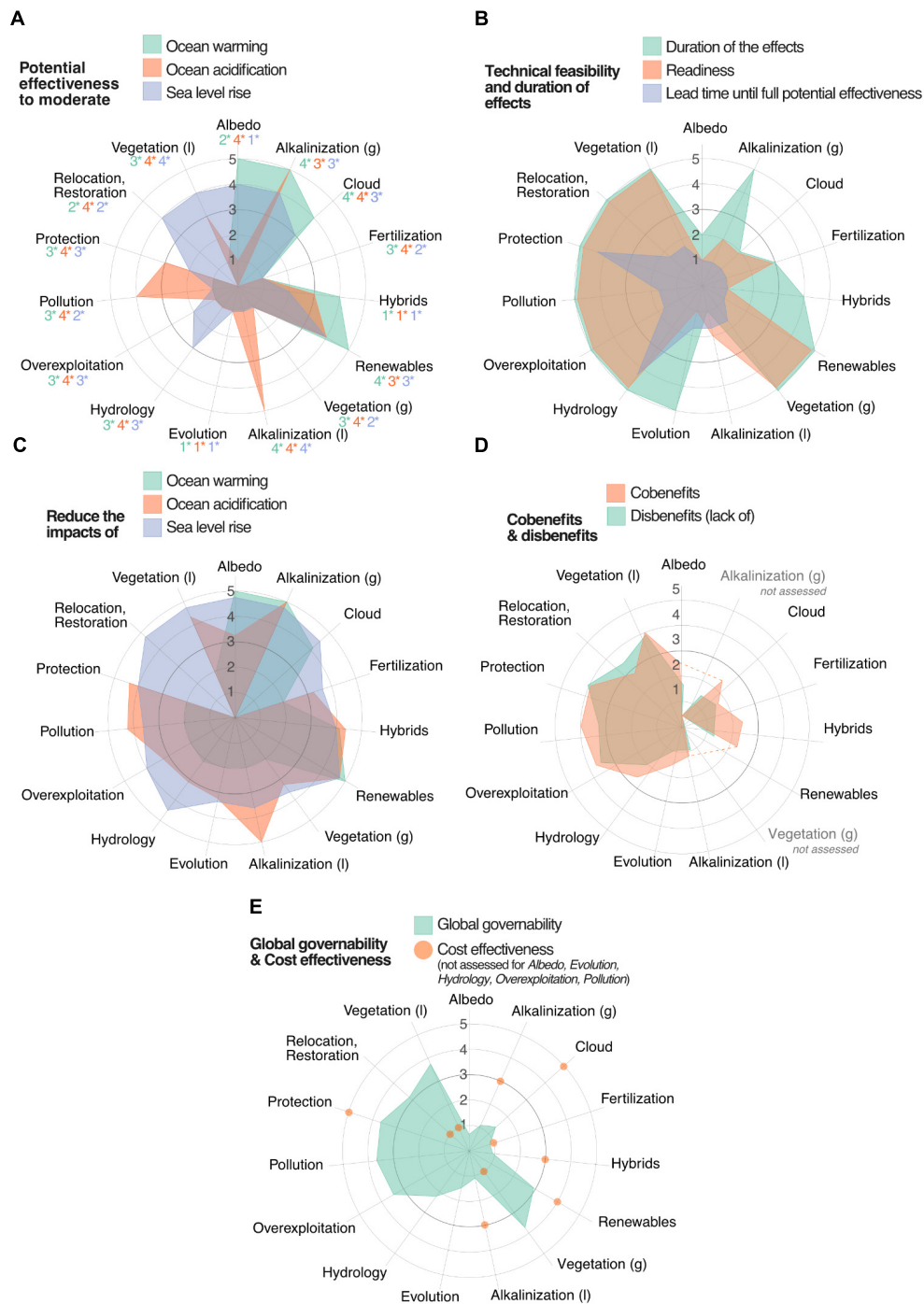


FIGURE 4 | Assessment of ocean-based measures to address key ocean drivers. Scores 1 to 5: very low, low, moderate (thicker circle), high, and very high. Confidence levels of the potential effectiveness to moderate ocean warming, ocean acidification, and sea-level rise are shown in panel (A) (1* to 5*; very low, low, moderate, high, very high; see section “SM2.1” of the **Supplementary Materials**). Details on the assessment can be found in section “SM3” of the **Supplementary Materials**.

moderate ocean warming, ocean acidification, and sea-level rise (Figures 2, 4A). Restoration of *vegetation* to increase CO₂ capture has a very low cost effectiveness but conservation of *vegetation* to avoid further emissions is very cost-effective. For

example, conserving mangroves to avoid further CO₂ emissions is considerably cheaper than restoring mangroves to enhance CO₂ uptake [4–10 vs. 240 US\$/t CO₂ (Siikamaki et al., 2012; Bayraktarov et al., 2016)]. *Cloud brightening*, *protection*, and

renewable energy have the highest cost efficiency while *albedo enhancement*, *vegetation* and *relocation and reef restoration* have the lowest. Note that cost effectiveness generally increases over time and with increasing scale of implementation, due to learning and economies of scale, and that there is uncertainty in many of these estimates (see section “SM3.5” of the **Supplementary Materials**) as reflected in the low levels of confidence. This generally is a consequence of lack of economic data from testing/deployment of many of these methods at relevant scales.

Global Governability

Governance is the “*effort to craft order, thereby to mitigate conflict, and realize mutual gains*” (Williamson, 2000) amongst actors from public, private, and civil society sectors. Here, we assess the governability of global and local ocean measures in terms of the potential capability of the international community to implement them, managing associated conflicts and harnessing mutual benefits (see section “SM2.9” of the **Supplementary Materials**). We focus on the international dimension of decision and action to reflect the global scope of the study, despite the fact that we recognize that global and local measures do not face the same constraints for implementation – e.g., bi- or multi-lateral diplomatic issues for the former (e.g., Smit, 2014; Cinner et al., 2016; Rabitz, 2016) and local institutional and population reluctance challenges for the latter (e.g., Cinner et al., 2016).

On that basis, the governability of a scheme increases with its effectiveness (Ostrom, 2007), the predictability of its effects (Hagedorn, 2008; Ostrom, 2009), its co-benefits, the absence of disbenefits together with the presence of national-level net benefits, the presence of enabling institutions and the absence of constraining institutions, and higher normative consensus amongst relevant actors (Abbott and Snidal, 1998; Barrett, 2005). Global governability is likely to be much higher when there are national-level net benefits (i.e., national benefits outweigh the negative environmental impacts and national costs of implementation), since single nation states may then implement measures without having to rely on international cooperation (Kaul et al., 1999). This is the case for *protection*, *vegetation* as well as for *relocation and reef restoration* (Figure 4E and section “SM3.6” of the **Supplementary Materials**). Conversely, ocean-based SRM measures (*cloud brightening* and *albedo enhancement*), while being more effective in addressing drivers globally, are considered to have low governability because their implementation generally involves international cooperation to solve the free-riding dilemma with regard to global public goods (Pasztor et al., 2017). Thus nations are likely to be reluctant to unilaterally take on extra costs that may reduce their own economic competitiveness (Preston, 2013; Rabitz, 2016; Williamson and Bodle, 2016). Additionally, SRM measures entail potentially significant disbenefits and high uncertainties (Figures 4D, 5; sections “SM3.4 and SM3.4.3” of the **Supplementary Materials**), which further reduce their present governability. *Renewable energy* is in an intermediate position: renewables are becoming more economically competitive compared with fossil-fuel based energy, thereby providing national-level incentives to implementation. Taken together, the scores exhibit a fundamental

tradeoff in climate policy: global measures are more effective than local ones in addressing the climate problem, but they are in general more difficult to implement due to challenges in global governance.

POTENTIAL TO REDUCE IMPACTS ON ECOSYSTEMS

Reducing the climate-related impacts depends on two attributes, the effectiveness to reduce exposure to warming, acidification, and sea-level rise (Figure 4A; sections “SM3.1 and SM3.2” of the **Supplementary Materials**) and the sensitivity of ecosystems to changes in these drivers (Figure 1; section “SM3.3”). Differences in these attributes lead to different reduction of impacts both among drivers and ecosystems (Figure 5). For example, *renewable energy* consistently scores very high in its combined effectiveness to reduce the impacts because it reduces exposure to all three drivers. In contrast, *relocation and reef restoration* is one of the less effective measures in reducing impacts because, despite the fact that restoration can reduce relative sea-level rise, it does not necessarily reduce exposure to ocean warming and acidification *in situ* unless the relocation involves species or habitat transfers to localities that are cooler and/or have higher pH. Another example is *albedo enhancement*, the effectiveness of which is very high to reduce the impacts of warming, high for sea-level rise and very low for acidification. Thus aside from solutions like massive and rapid deployment of marine renewable energy, multiple and in some cases non-traditional solutions targeting different drivers may be needed, the combination of which will be ecosystem-specific. For example, solutions that target warming and acidification are more important to reduce the impacts on coral reefs and Arctic biota, whereas solutions that are most effective to reduce the impacts of sea-level rise will be more relevant for mangroves and saltmarshes.

While the most effective measures to reduce exposure to all three drivers are the global ones (Figure 4A), they do not generally reduce the sensitivity of the ecosystems to climate-related drivers. In contrast, local solutions have low or moderate effectiveness to reduce changes in climate-related drivers. They aim to moderate impacts primarily through reducing non-climatic drivers that affect the health and resilience of coastal ecosystems and marine environments such as pollution, overexploitation, overfishing, and coastal development (Halpern et al., 2015). Thus, local solutions have a high level of co-benefits and generally induce a low level of disbenefits since many have a long history of successfully mitigating non-climate stressors – the value of which is considered in this study as co-benefits (Figure 5). The most effective measures across all ecosystems (high to very high effectivenesses to reduce the impacts of ocean warming, ocean acidification, and sea-level rise; Figure 4C) are *renewable energy*, *alkalinization*, *hybrid methods*, *vegetation* (local) and *albedo enhancement*, with *renewable energy* showing the greatest combined effectiveness. *Protection*, *restoring hydrology*, and *eliminating overexploitation* also score relatively high to reduce impacts on seagrass habitats, mangroves and saltmarshes (Figure 5). *Relocation and reef restoration* and *cloud brightening* consistently have the lowest

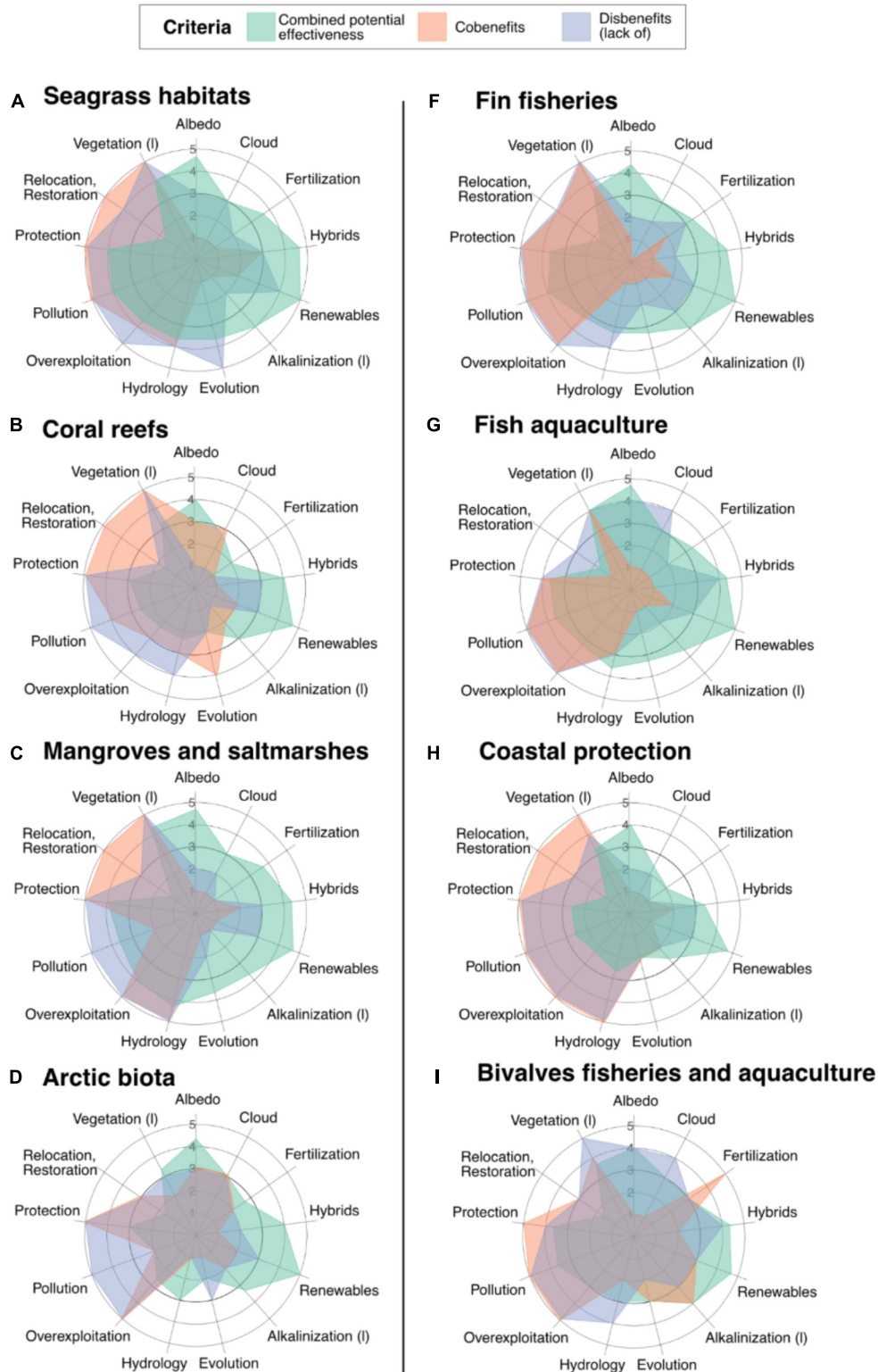


FIGURE 5 | Contribution of ocean-based solutions to reduce the impacts of key ocean drivers on key ecosystems (**A–D**) and ecosystem services (**E–H**). The combined potential effectiveness represents the average potential effectiveness to reduce the impacts of ocean warming, ocean acidification, and sea-level rise (see section “SM3” of the **Supplementary Materials**). Scores 1 to 5: very low, low, moderate (thicker circle), high, and very high.

combined potential effectiveness; however, if reef restoration were considered separately from relocation, it would score higher (especially with regard to reducing local relative sea-level rise).

The potential to reduce the impacts of non-climatic drivers is a key attribute of local measures because it increases the resilience of ecosystems to climate change (O'Leary et al., 2017). For example, *protection* and *eliminating overexploitation* can support high reproductive outputs and juvenile recruitment following climate-related mass mortalities, allowing for population recovery from extreme events (Micheli et al., 2012; Roberts et al., 2017). Moreover, these measures produce co-benefits, such as spillover benefits of MPAs to adjacent areas supporting shellfish fisheries and aquaculture, and few, if any disbenefits, especially for coral reefs and vegetated marine habitats (Roberts et al., 2017). Some MPAs are more affected by coral bleaching than fished areas because they harbor more thermally sensitive corals (Graham et al., 2008) but there is a strong case that protected coral reefs recover better (Cinner et al., 2013).

Whilst local solutions can decrease the total (climate- and non-climate related) impacts and improve ecosystems' resilience, they cannot eliminate all of the climate-related component of impacts. For example, water quality and fishing pressure had minimal effect on the unprecedented bleaching of 2016 (Hughes et al., 2017b). Furthermore, and despite local protections, the changes associated with a high CO₂ emission scenario will result in further habitat and species losses throughout low-latitude and tropical MPAs, for example through the effects of warming on habitat-forming species such as corals, thereby reducing their beneficial roles (Bruno et al., 2018).

Despite the fact that most solutions implemented at local scales have a limited effectiveness to reduce the impacts of warming, acidification, and sea-level rise globally, they all have some beneficial effects, which could help in countering global climate impact if scaled beyond their current implementation. For example, seaweeds and seagrasses can reduce ocean acidification locally (e.g., Unsworth et al., 2012; Mcleod et al., 2013) and can potentially buffer adjacent coral populations by off-setting decreases in seawater pH (Camp et al., 2016).

POTENTIAL TO REDUCE IMPACTS ON ECOSYSTEM SERVICES

Sensitive ecosystem services are also expected to benefit from the implementation of measures that have the highest potential effectiveness in addressing climate drivers globally, such as *renewable energy* and *alkalinization* (Figure 4A). Our assessment, however, suggests that these measures may also lead to significant disbenefits (Figures 5B–E, sections “SM3.4 and SM3.4.3” of the **Supplementary Materials**). For instance, the addition of non-carbonate alkaline minerals may perturb biogeochemical processes through the release of mineral constituents such as cadmium, nickel, chromium, iron, and silicon (Hartmann et al., 2013). This may alter the pattern of primary and secondary production, and increase contaminant accumulation along the food chain (Russell et al., 2012; Alava et al., 2017), possibly

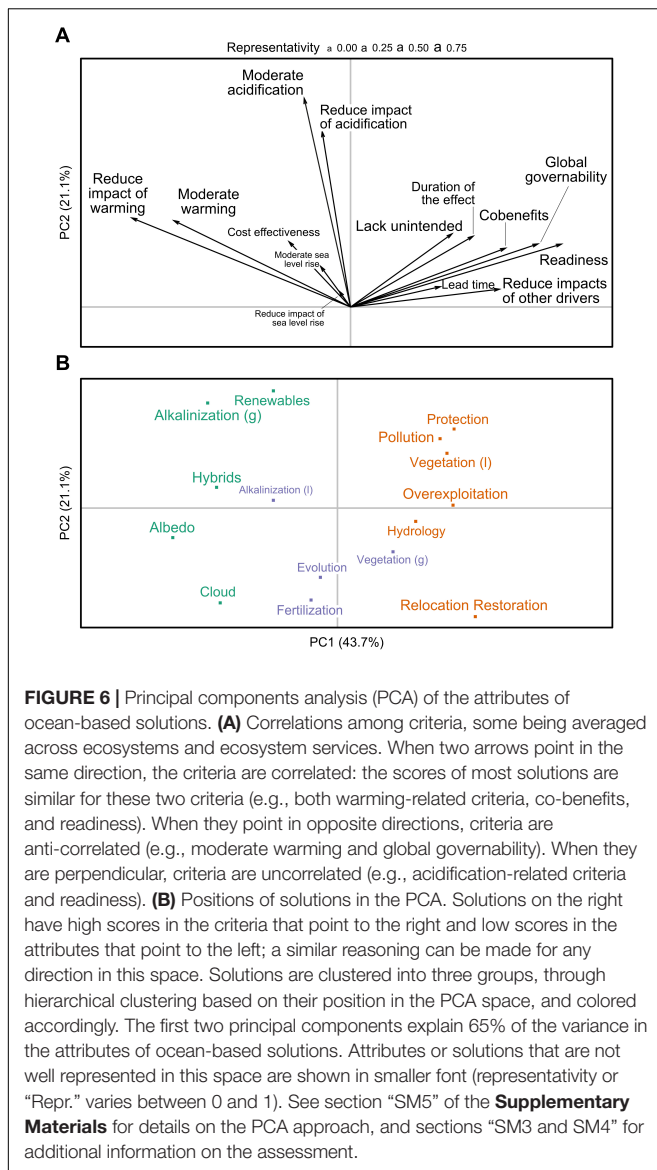
impacting fisheries and aquaculture production, and the coastal protection value of coastal habitats. Furthermore, *alkalinization* is only moderately effective in reducing the impacts of sea-level rise, which is the primary driver affecting mangroves and saltmarshes. A similar conclusion applies to most of the global measures, notably *cloud brightening* and *albedo enhancement*, where large-scale deployment may risk high levels of disbenefits. In contrast, although our assessment suggests that large-scale *renewable energy* may lead to some local collateral damages on ecosystem services when these systems are deployed in coastal ecosystems, these impacts may be largely moderated through careful planning and consultation (Pelc and Fujita, 2002). In contrast, minimal damage is anticipated for deep-water floating systems currently being tested.

Measures that are most effective to reduce climate-related drivers locally (e.g., relative sea-level rise) often also have the dual benefit of minimizing the impacts from non-climatic drivers affecting coastal and marine ecosystems and environments (e.g., pollution, overexploitation, overfishing, and coastal development). As a result, the most effective local-scale interventions to maintain healthy conditions for fin fisheries, fish and bivalve aquaculture, and coastal protection are *eliminating overexploitation*, *restoring hydrology*, *reducing pollution*, *vegetation*, and *protection* (Figure 5). Modeling studies indeed suggest that the increase in stock abundance and productivity by effective management of fisheries and conservation of fish stocks (Costello et al., 2016) is likely to compensate losses from climate change (Cheung et al., 2017). It was shown that sustainable mangrove management interventions support surface elevation gains, thus limiting relative sea-level rise (Sasmito et al., 2016). More generally, *protection* and *vegetation* enable mangroves, saltmarshes, coral reefs, and seagrass to reduce the impacts of sea-level rise on coastal communities through wave attenuation and shoreline stabilization. Maintaining the health of ecosystems that provide coastal protection also has significant additional co-benefits to local human communities (e.g., carbon sequestration, water filtering, tourism, food security, recreation; Barbier et al., 2011; Weatherdon et al., 2016), in addition to supporting their resilience to climate impacts (Carilli et al., 2009). It is not surprising then that many countries are actively including marine ecosystems in their national climate plans as shown by the Nationally Determined Contributions submitted under the Paris Agreement (Gallo et al., 2017).

PATHWAYS TO IMPLEMENTATION

Clusters of Potential Solutions and Tradeoffs

A principal components analysis (see section “SM4” of the **Supplementary Materials**) was used to reduce the eight dimensions of our assessment dataset defined by the scoring criteria to two latent dimensions that explain most of the variance in the assessment data. Three clusters of schemes emerge (Figure 6). The first one includes *alkalinization* at the global scale, *hybrid methods*, *albedo enhancement*, and *cloud brightening*,



which show high potential effectiveness to reduce warming and acidification, and their impacts. However, there has been relatively little research, testing and application on such solutions, and they generally score low for technological readiness, co-benefits, lack of disbenefits, and global governability. In contrast, the second cluster includes almost all local measures (*protection*, *reducing pollution*, *vegetation* at the local scale, *eliminating overexploitation*, *restoring hydrology* and *relocation and restoration*), and is characterized by low effectiveness to reduce warming and its impacts, and moderate effectiveness to reduce ocean acidification and relative sea-level rise and their impacts. These measures are, however, technologically ready, have significant co-benefits, few disbenefits and can also help to reduce the impacts of non-climatic drivers. *Renewable energy* stands apart as it exhibits both high potential effectiveness and technology readiness, thus ranging in between clusters 1 and 2. The third cluster includes *assisted evolution*, *alkalinization* at the

local scale and *fertilization*, which have low to moderate scores across most criteria assessed.

Ocean Governance Challenges

Measures which are the most technically feasible also have the highest global governability (**Figure 4**). They comprise *protection*, *eliminating overexploitation*, *reducing pollution*, *vegetation*, *relocation* and *reef restoration*, and *renewable energy*. Except for the latter, all these measures are local. Their governability is high to very high except for *restoring hydrology* and *assisted evolution* (moderate or low). Global measures such as *albedo enhancement*, *fertilization*, *hybrid methods*, *cloud brightening*, and *alkalinization* have a lower overall technical feasibility, partly due to lack of testing and experience, together with moderate to low governability. Yet none of these schemes do much to reduce or moderate the impacts of the climate-related drivers considered in this study (ocean warming, ocean acidification and sea-level rise).

Such conclusions highlight the need for multiple-scale and multiple-stakeholder initiatives, hence calling for improved international governance mechanisms to ensure coherency in ocean-based climate action. These governance challenges are, however, constrained by controversies on the potential solutions, which scientific investigations and policy engagement can help overcome. Controversies are mostly in the “addressing the causes of climate change” and “solar radiation management” areas of action (**Figure 2**). They include: the moral hazard dilemma, i.e., that development and deployment of alternative solutions might decrease effort on emission reductions (Preston, 2013; McLaren, 2016); the risk of premature lock-in of suboptimal solutions and path dependencies (Burns et al., 2016; Reynolds et al., 2016); and concerns regarding controllability and transnational effects (Williamson and Bodle, 2016). Ethical issues are also important, relating to informed consent and potential adverse impacts on countries unable to deploy such measures (Svoboda, 2012; Suarez and van Aalst, 2017; Rahman et al., 2018); and vested interests, as production and deployment of innovative measures could be a highly profitable market (Preston, 2013). Controversies related to the “protection of biota and ecosystems” and “manipulation to enhance biological and ecological adaptation” areas of action mostly arise from conflicts relating to local, national and global-scale interests, and the balance between short-term and long-term benefits and disbenefits (Cooley et al., 2016; Cormier-Salem and Panfili, 2016). Such trade-offs between “winners” and “losers” highlight the influence of social norms and values that may differ greatly between different stakeholders (Hopkins et al., 2016; Lubchenco et al., 2016). Testing the veracity of such perceptions via further research and demonstration of novel measures at relevant scales will clarify governance issues.

The Way Forward

The global implementation or testing of *renewable energy*, *fertilization*, *vegetation*, *eliminating overexploitation*, and *protection* has accelerated sharply in the past two decades (**Figure 3**). In particular, several local measures (*vegetation*, *protection*, and *eliminating overexploitation*) may achieve their full potential in a few decades at their current rate of deployment.

Nevertheless, the scale of deployment for most solutions remains far below what would be necessary to effectively address climate change drivers and impacts (**Figure 4B**). Delivering the full potential of global measures such as *renewable energy*, *alkalinization*, and *hybrid methods* requires orders-of-magnitude increases in their research, testing, and deployment. Such action is considered urgent on the basis of the climatic threats to ocean sustainability (Gattuso et al., 2015), and since there are decadal lag times until full maximum effectiveness of all the global measures considered here (**Figure 4B** and section “SM3.1” of the **Supplementary Materials**). In the meantime, there will likely be significant increases in climate-related impacts on ocean ecosystems and services, which will reduce ecosystems’ ability to provide local solutions (Albright et al., 2016; Cheung et al., 2016; Cinner et al., 2016), thereby decreasing leeway for action (Gattuso et al., 2015).

It is clear that the familiar and conventional marine management strategies cannot fully counter climate change and its impacts. Accelerating research and deployment of other potential solutions will, however, challenge the capacity of science, policy, and decision-making in evaluating and deploying solutions. Defining road maps to drastically enhance action faces major constraints relating to the large uncertainties in key non-climatic variables. Thus socioeconomic conditions may flip the balance between fossil fuel markets and renewables, potentially catalyzing a rapid acceleration of the deployment of marine renewables, but not necessarily with adequate consideration of local disbenefits. There is also a need to consider a broader range of measures than those assessed here, many of which are still in their infancy and unfamiliar to marine management (e.g., large-scale seaweed aquaculture, or abiotic methods of removing or stripping CO₂ from seawater). This calls for the development of policies and funding to foster and promote research into new or emerging ocean and climate management options.

OUTLOOK

Current pledges under the Paris Agreement are insufficient to hold the global average temperature increase to well below 2°C above pre-industrial levels, calling for a dramatic increase in global mitigation effort. However, even with a full and timely implementation of the Agreement, major impacts on sensitive marine ecosystems such as coral reefs and Arctic biota are expected, requiring additional, ambitious and rapid actions to address climate-related drivers locally, minimize their impacts, and increase resilience. To support efforts to address the ocean’s potential contribution to these mitigation and adaptation goals, our assessment highlights five evidence-based key messages.

First, each measure has tradeoffs. For example, *alkalinization* scores high in global mitigation potential, but low in technological readiness or global governability. In contrast, measures implemented locally such as *protection* and *reducing pollution* have strong co-benefits and high governability, but have a much lower effectiveness to moderate changes in climate-related drivers. Decisions favoring any measure must therefore consider multiple criteria, including effectiveness, feasibility, co-benefits, disbenefits, governability, and cost effectiveness,

rather than only the climate-related effectiveness or cost effectiveness.

Second, ocean-based measures with relatively high global effectiveness (such as *albedo enhancement*) have significant adverse side effects on key marine ecosystems and services. In contrast, local measures rank higher in terms of global governability, co-benefits and lack of disbenefits, and have a moderate ability to reduce climate-related impacts, only offering local opportunities for mitigation. The emerging picture is that actions in addition to local and more conventional marine management are needed to increase chances of avoiding or countering climate impacts. It is unlikely that a single measure will be able to meet a pathway consistent with the Paris Agreement. The introduction of multiple measures, including land-based ones, would require deployment of each of them at decreased scales relative to single-measure deployments, and would also reduce the risk of side effects (see also Minx et al., 2018).

Third, some measures that offer greater effectiveness in countering climate and its impacts (e.g., *alkalinization*, *cloud brightening*, *albedo enhancement*, and *assisted evolution*) currently exhibit too many uncertainties to be recommended for large-scale deployment until more research is conducted. However, measures with demonstrated potential effectiveness, co-benefits and with no or few disbenefits (*renewable energy* as well as other local solutions except *assisted evolution*) are no-regret measures that can be widely deployed immediately, as other potential solutions are explored. The high merits of *renewable energy* is consistent with the conventional policy approach that the best way to avoid climate impacts (on the marine environment, as well as elsewhere) is to eliminate the primary driver, excess atmospheric CO₂ concentration, by drastically reducing CO₂ emissions (Gattuso et al., 2015).

Fourth, climate change intervention at multiple scales requires that multiple and diverse actors are involved, hence calling for coordination across scales. Interestingly, besides being central to decisions on global measures, our assessment suggests that the international community can also play an indirect supporting role to the implementation of local solutions. The international community must therefore accelerate diplomatic and political efforts, especially within institutions such as the UNFCCC and the UN Convention on Biological Diversity, to improve existing arrangements or find new ones, and develop facilitative mechanisms for global to local action.

Fifth, since there are controversies and uncertainties on many of the measures we considered, a better scientific understanding of solution benefits, disbenefits, costs, and suitable governance arrangements is needed to inform policy and decision making. For example, 41% of the scores have low to very low levels of confidence (see section “SM3.4” of the **Supplementary Materials**). A major area of research thus relies in better determining potential effectiveness, cost-effectiveness, and desirability under various greenhouse gas emission scenarios. Furthermore, given the social challenges involved in all potential solutions, social science research is needed for understanding factors that hinder or promote effective and fair governance of ocean-based solutions (Magnan et al., 2016). In turn, this will allow a balanced consideration of new, unconventional

ideas (e.g., regional cloud brightening to reduce pressures on coral reefs, advanced hybrid technologies, or innovative governance solutions for reconciling social conflicts associated to measures). This is a prerequisite for providing decision- and policy-makers with robust information, for example through the various products of the sixth assessment cycle of the IPCC. As new knowledge and insights become available, it is key that scientists effectively engage with the general public and decision makers, especially discussing the potential, feasibility, tradeoffs and social preferences of specific measures, and the consequences of failing to deploy solutions on time. This will notably help to increase mutual understanding and serve to reduce confusion and misinformation regarding the realized and future impacts of climate change on the ocean (Gelcich et al., 2014).

CONCLUSION

Both the marine policy and science communities need to recognize the uncertainties and limitations of currently available climate and ocean management options; support the immediate development of the most promising ones, e.g., *renewable energy* and local actions that can be scaled up; and acknowledge that new or emerging measures that are not part of current marine management practice might, through further research and testing, prove cost-effective as well as environmentally and socially acceptable.

AUTHOR CONTRIBUTIONS

J-PG, AKM, LB, WWLC, CMD, JH, EM, FM, AO, PW, RB, VIC, RDG, JJM, H-OP, and GHR designed and carried out the research. All co-authors conducted the analyses and wrote the paper.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2018.00337/full#supplementary-material>

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